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A ZOOGEOGRAPHICAL SINGULARITY AT WEAVERS CREEK, TASMANIA

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Abstract

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A narrow landscape zone containing the range boundaries of at least six widespread millipede species and two widespread centipede taxa has been mapped at Weavers Creek, near Launceston in northern Tasmania. Two other, geographically restricted millipede species are unusually abundant in the zone. Although the zone coincides with a broad ecotone between dry and wet eucalypt forest, its existence is most plausibly explained as the result of interspecific competition and historical factors. Weavers Creek is neither a 'centre of endemism' for litter invertebrate diversity nor the site of unusual forest habitats. The area is nevertheless of considerable conservation significance because of the insights it affords into ecological parapatry and local-scale invertebrate evolution.

Introduction

The East Tamar Break in north-east Tasmania is a c. 50 km-long faunal boundary respected by a range of litter invertebrates (Mesibov, 1994a). In this article I report progress in mapping millipede distributions near the southern end of the East Tamar Break, where a boundary c. 5 km wide passes through a large block of lightly disturbed native forest in the Weavers Creek catchment, south-west of Mt Barrow. This portion of the Break, it is argued, should be conserved as a field laboratory for studies of parapatry and invertebrate evolution.

Methods

Between December, 1991 and December, 1995 I searched for polydesmidan millipedes at 154 sites within a 30 × 30 km study area just east of Launceston (Figs 1 and 2). Millipedes were hunted in rotting logs, in and under leaf litter and stones, and in the top layers of richly organic soil. Hand-collecting is a more efficient method for sampling millipedes than pitfall-trapping (Mesibov et al., 1995) and is particularly well-suited to sampling in small remnants of native bush, where millipedes may be concentrated in a few square metres of suitable habitat. My by-catch included chordeumatidan and polyzoniidan millipedes, centipedes and velvet worms. All collections have been lodged at the Queen Victoria Museum and Art Gallery (QVMAG) in Launceston. Specimens of the undescribed millipedes and centipedes referred to in this paper have been registered as sorted taxa (e.g., *Lissodesmus* n. sp. E1 pending further taxonomic study.

Geographical overview

Mt Barrow stands at the high, eastern edge of a tilted and block-faulted sheet of Jurassic dolerite (Longman, 1966). Drainage west of Mt Barrow is partly controlled by north-north-westerly-trending faults, as exemplified by Weavers Creek and the St Patricks River within the study area (Fig. 3). The narrow rectangle in Fig. 3 was drawn perpendicular to the fault trend, and mid-point elevations were noted (from 1:25000 topographic maps) on 1 km-wide strips across the

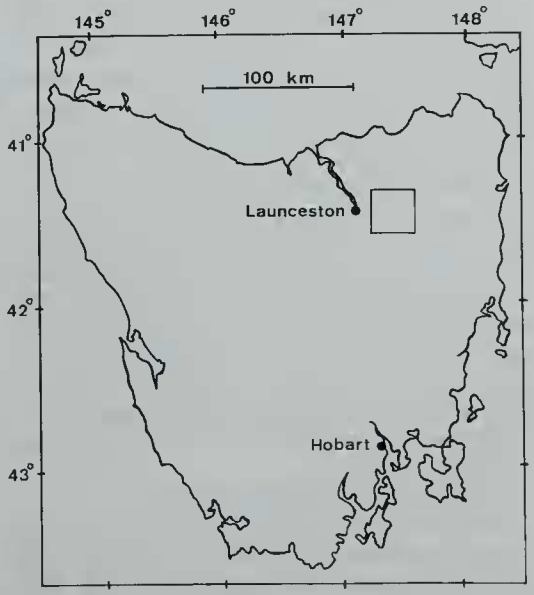

Figure 1. Location of the 30 x30 km study area, just east of Launceston.

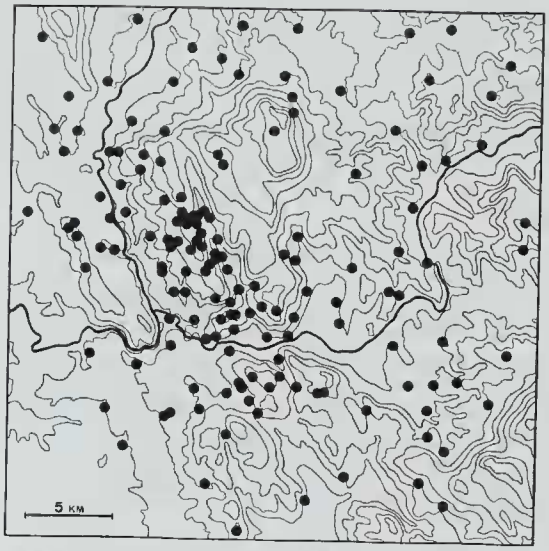

Figure 2. Distribution of sampling sites in the study area (to 8 December 1995).

width of the rectangle every 250 m from its western end. The resulting elevation profile (Fig. 4) clearly shows the step-faulted structure of the Weavers Creek area. For convenience in description I have given the name 'Weavers Ridge' to the long hill between Weavers Creek and the St Patricks River. At the southern end of Weavers Ridge, Weavers Creek abruptly abandons a major fault line and turns west to join the North Esk River (Fig. 3).

Early Tertiary deposits in the long basins between fault blocks in the Tamar area are generally flat-lying and unfaulted, indicating that faulting and tipping of the dolerite masses occurred prior to the early Tertiary (Longman, 1966). Minor eruptions of Tertiary basalt at Nunamara and Watery Plains are believed to have diverted the St Patricks and North Esk Rivers into their present courses (Longman, 1966), but the general structure of the landscape in the study area appears to have been stable through most of the Tertiary. Although Mt Barrow is not thought to have been glaciated during the Pleistocene (Caine, 1983), periglacial effects were severe and much of Weavers Ridge is mantled with frost-shattered dolerite debris and solifluction colluvium (Mesibov, unpublished observation).

The steep elevation gradient in Fig. 4 is paralleled by a steep gradient in annual rainfall (Fig. 5) and by a transition from dry eucalypt forest and woodland on the Tressick Hills (Fig. 4) to wet eucalypt forest on the western, lower slopes of Mt Barrow. A broad ecotone between dry and wet eucalypt forest covers Weavers Ridge. In the general vicinity of Weavers Creek, all native plant cover is eucalypt forest apart from alpine scrub on Mt Barrow (treeline c. 1100 m) and riparian strips of *Nothofagus*-dominated rainforest on the Creek itself and its tributaries on the Mt Barrow side. Very little of the steeper ground in the study area has been cleared for agriculture (Fig. 6), but grazing and frequent burning over the past 150 years have degraded the dry eucalypt forest on the Tressick Hills and the wooded hills south of the North Esk. The whole of the uncleared portion of the study area (apart from alpine scrubs and screes) was forested in pre-European times, and nearly all that forest has been selectively logged (in places repeatedly) and naturally regenerated. Small plantations of *Pinus radiata* and *Eucalyptus nitens* have been developed in recent years on non-rocky ground within the study area, but much of the uncleared land in Fig. 6 carried weed-free native forest in 1995, with a variably abundant litter fauna.

Distributions of polydesmidan millipedes

Polydesmidan or 'flat-backed' millipedes are the most species-diverse and abundant Diplopoda in Tasmania (Mesibov, 1994b). The most speciose local genus is *Lissodesmus* Chamberlin in the Dalodesmidae, with at least 25 Tasmanian and 3 Victorian species (Mesibov, in preparation). Several species of *Lissodesmus* in the study area are shallow-burrowing in soil and deep litter (Table 1). *L. adrianae* Jeekel, 1984 is a north-east Tasmanian endemic with a western range boundary at the East Tamar Break (Fig. 7) and an apparent preference for very moist microhabitats. The more ecologically tolerant *L. alisonae* Jeekel, 1984 (Table 1) has its eastern range boundary at the Break (Fig. 8). *Lissodesmus* n. sp. E1, a widespread eastern species, is parapatric with *L. alisonae* at the latter's southern limit (Figs. 8, 9) and overlaps fairly broadly with *L. adrianae* (Figs. 7, 9), although *adrianae*/E1 parapatry has been documented near Mt Horror and Rayners Hill in north-east Tasmania (Mesibov, unpublished observations). These three species of *Lissodesmus* meet at a distributional 'triple point' near the southern end of Weavers Ridge (Figs. 7, 8, 9).

Lissodesmus n. sp. NE1 and the unrelated dalodesmid *Tasmanodesmus hardyi* Chamberlin, 1920 are morphologically convergent (Table 1) and adapted for life in loose litter and cavities in rotting logs. *T. hardyi* is widespread in

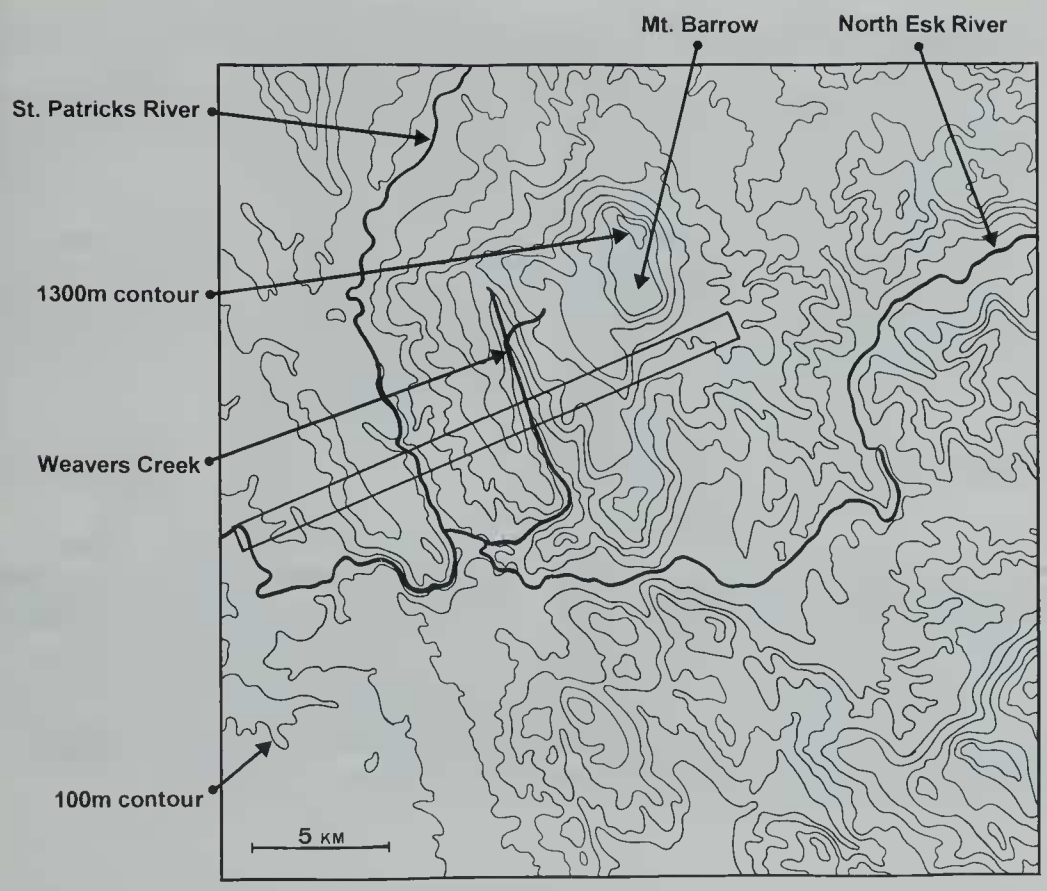

Figure 3. Features of the study area. St Patricks River and Weavers Creek are tributaries of the west-flowing North Esk River. Narrow rectangle defines the elevation transect in Fig. 4 (see text for details). Contour interval is 100 m.

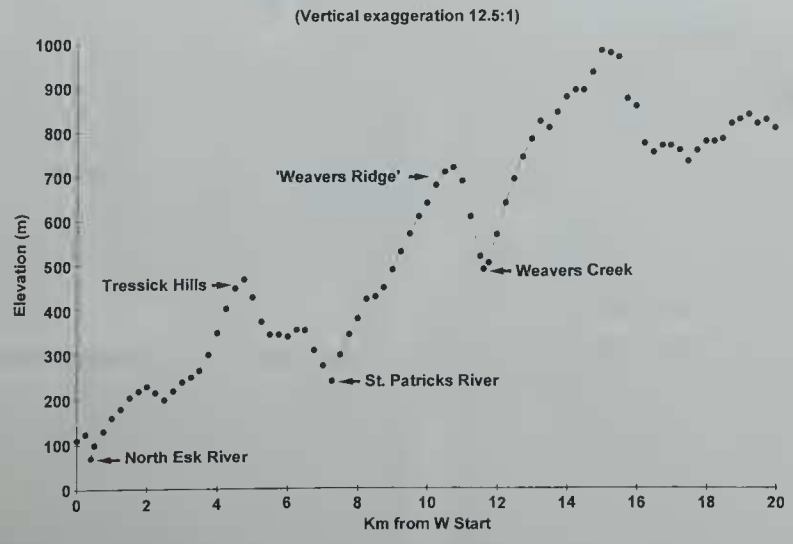

Figure 4. Elevation transect along narrow rectangle in Fig. 3 (see text for details).

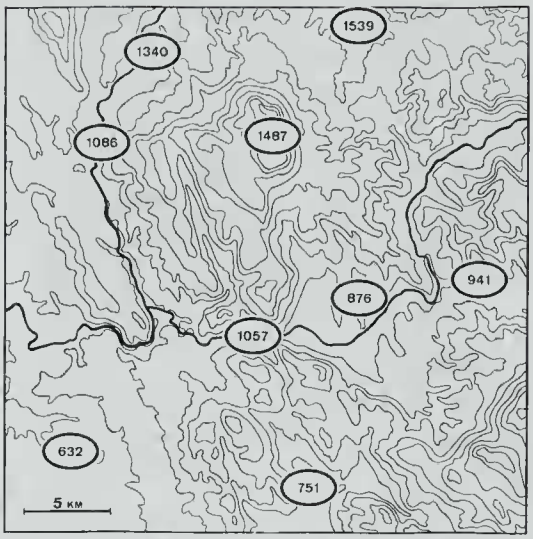

Figure 5. Annual rainfall in millimetres in the study area (data courtesy Bureau of Meteorology). Clockwise from the south, the stations and years of record are: '751', Deddington-Nile River (63 years); '632', Evandale-Ridgeside (58), '1086', combined Nunamara (15 and 30), '1340', St Patricks River (83), '1487', combined Mt Barrow (6 and 12), '1539', Diddleum Plains (33), '941', Blessington-Heathcote (22), '876', Burns Creek-Janefield (21), '1057', Musselboro-Aplico (40).

Figure 6. Extent of clearance for agriculture (stippled) in the study area, based on Landsat images (January, 1994). Apart from small areas of alpine vegetation, all uncleared land has tree cover. Woodland adjacent to cleared ground, especially in the south-west of the study area, has been degraded by grazing and frequent burning. A small and scattered proportion of the forested area (c. 10%) has been converted to plantations of non-native trees in recent years.

Tasmania (Fig. 10) while *Lissodesmus* n. sp. NE1 is a north-east Tasmanian endemic (Fig. 11). The two distributions abut at the East Tamar Break.

A sixth widespread polydesmidan occurring in the study area is a distinctive but undescribed paradoxosomatid (n. gen., n. sp.) found throughout much of eastern Tasmania (Fig. 12) in open forest, woodland and scrub, where it is sometimes day-active (Mesibov, unpublished observations). It has not been found east of the East Tamar Break in the study area (Fig. 12).

Two dalodesmids with restricted distributions also occur in the study area. The first is in an undescribed genus with three widely disjunct species in Tasmania (Mesibov, in preparation). This species, here called dalodesmid n. gen. 2, n. sp. 2, is a deep-burrowing form rarely seen in the litter layer; it is particularly abundant in the study area (Fig. 13) and persists in tiny bush remnants (<0.5 ha) on local farms. The second dalodesmid is *Lissodesmus* n. sp. NE3, known only from one site outside the study area but locally abundant at sites near Weavers Creek (Fig. 14). *Lissodesmus* n. sp. NE3 is intermediate in sexual characters between *Lissodesmus* n. sp. E1 and *L. alisonae* and may represent a stabilised hybrid taxon (Mesibov, in preparation).

A consensus sketch of the East Tamar Break in the Weavers Creek area, drawn from the distributions just reported, is offered in Fig. 15. Range boundaries within this zone of overlap run from c. 300 to c. 700 m elevation, chiefly along Weavers Ridge in the broad dry/wet eucalypt ecotone. The south-western edge of the zone roughly coincides with the 1000 mm isohyet (Fig. 5).

Distributions of other litter invertebrates

To date, no litter macroinvertebrates other than millipedes and centipedes have been intensively mapped in the study area by specialist collectors, although snails, amphipods, isopods, spiders, harvestmen, carabid beetles and neanurid collembolans are all locally abundant. I am currently sorting the smaller Tasmanian Polydes-

Table 1. Some features of millipede species mapped in this article. (Rainfall ranges estimated from isohyet maps.)

Species	Elevation Range (m)	Rainfall Range (mm)	Characters	Microhabitat
Lissodesmus adrianae	60–1050	850–1700	15–20 mm long;	deep moist litter,
Lissodesmus alisonae	10–1010	650–1500	reduced paranota;	upper horizon of
Lissodesmus n. sp. E1	10–840	600–1100	lightly pigmented	organic-rich soil
Lissodesmus NE1	20–790	800–1700	25–30 mm; wide	loose moist litter,
Tasmanodesmus hardyi	10 -1120	600–2000	paranota; long, thin legs; purple-brown pigmentation	cavities in moist rotting logs
paradoxosomatid, n. gen. n. sp.	50–1120	600–1100	20–25 mm; very reduced paranota; heavily sclerotised cuticle; dark brown or black	loose dry or wet litter; under bark and stones
dalodesmid, n. gen. 2, n. sp. 2	270–1000	700–1200	20–25 mm; very reduced paranota; heavily calcified cuticle; lightly pigmented	deeper layers of organic-rich soil, deep in wet rotting logs
Lissodesmus n. sp. NE3	350–710	700–1000	15 mm; partly reduced paranota; lightly pigmented	as *L. adrianae*

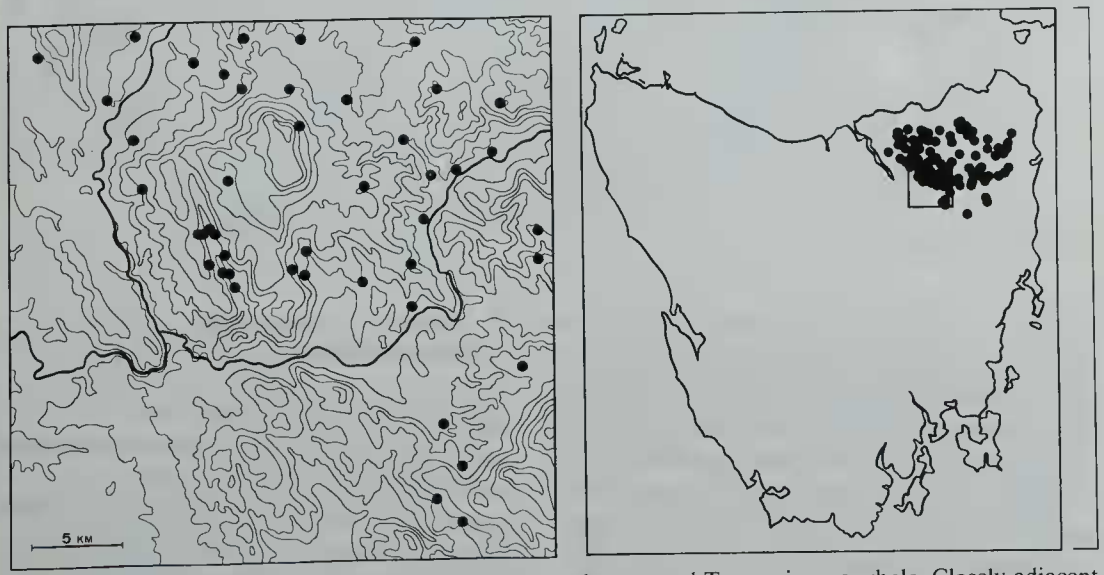

Figure 7. Distribution of *Lissodesmus adrianae* in the study area and Tasmania as a whole. Closely adjacent localities on the State map have been marked with a single dot. Localities are those known as of 8 December 1995.

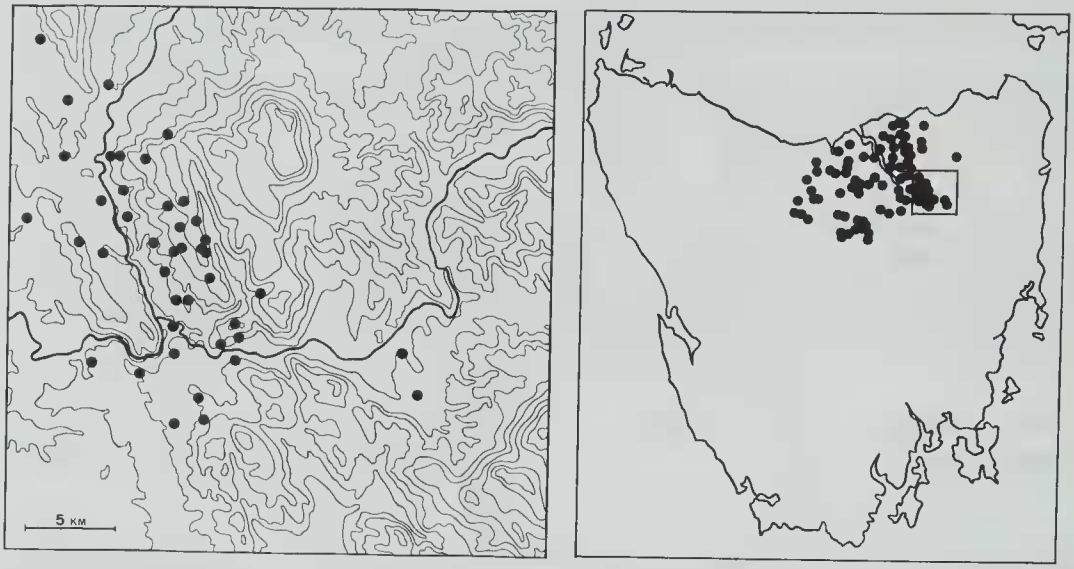

Figure 8. As Fig. 7, for *Lissodesmus alisonae*.

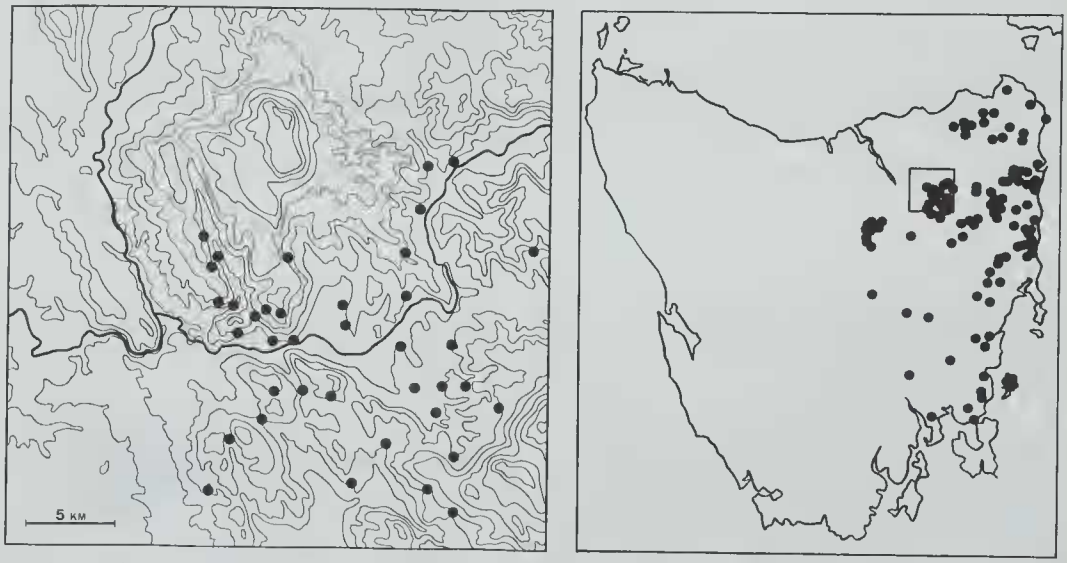

Figure 9. As Fig. 7, for *Lissodesmus* n. sp. E1.

mida to morphospecies and looking for additional distributional congruences in the study area. A preliminary sorting of geophilomorph centipedes in the genus *Tasmanophilus* is being carried out in collaboration with R.L. Jones (Kings Lynn, UK) and a distinctive new species with 41–45 leg pairs, here called *Tasmanophilus* n. sp., is known to be a northeast regional endemic (Fig. 16). All other local *Tasmanophilus* species (the *T. 'opinatus'* group) have 49 or more pairs of legs; their combined distributions in the study area are shown in Fig. 17. The overlap again appears to be concentrated on Weavers Ridge.

Why Weavers Creek?

It is unwise to assume that all the range boundaries concentrated in the Weavers Creek area are there for the same reason. The simplest explanation for the paradoxosomatid (n. gen., n. sp.) range limit is that this species prefers open forest, and that denser understorey vegetation on the Mt Barrow side of Weavers Creek is unfavourable habitat and a dispersal barrier.

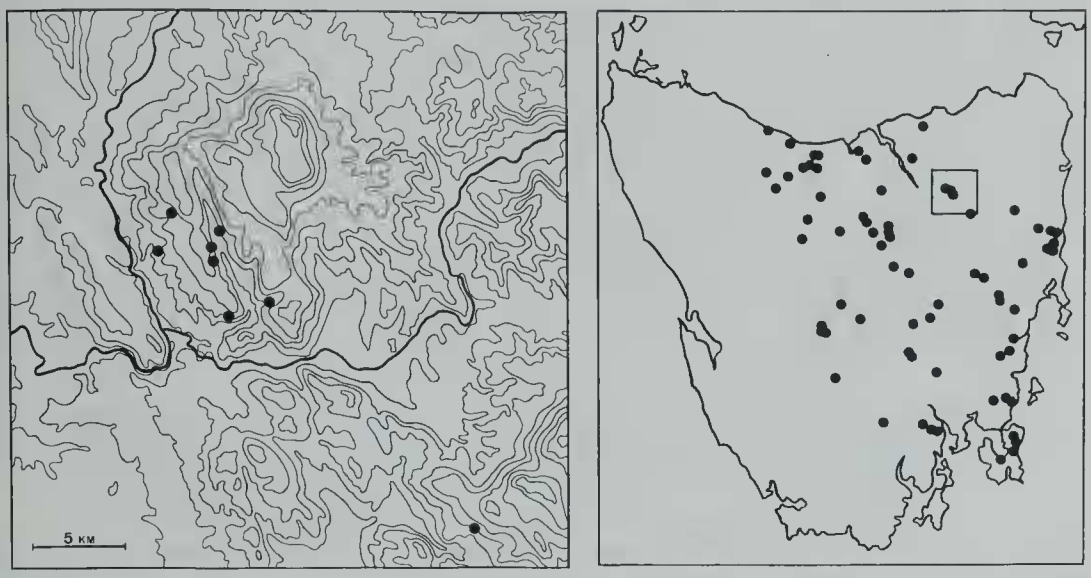

Figure 10. As Fig. 7, for *Tasmanodesmus hardyi*.

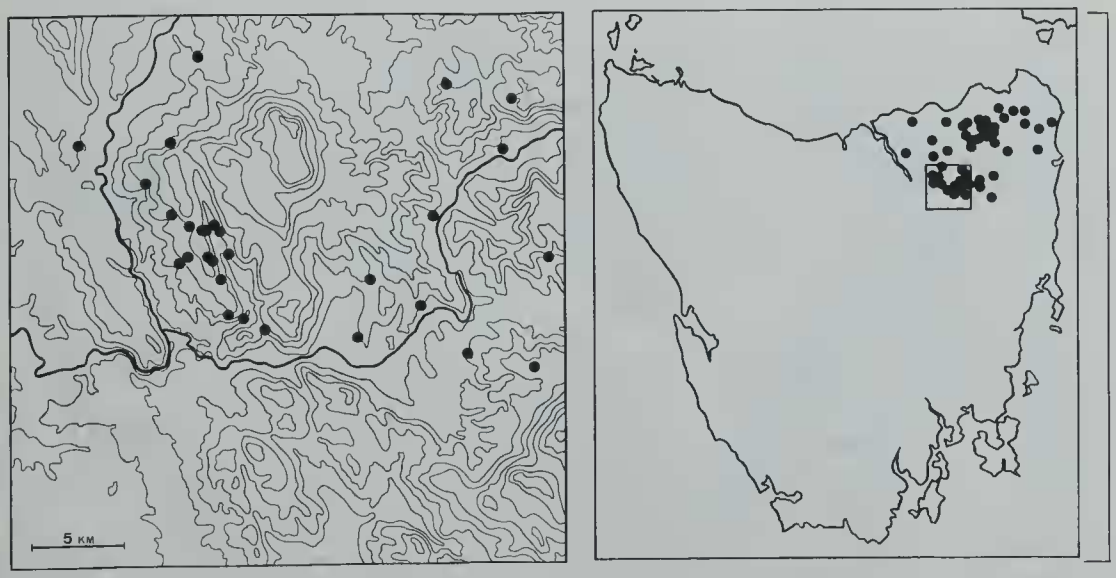

Figure 11. As Fig. 7, for *Lissodesmus* n. sp. NE1.

Habitat preference fails as an explanation for *Lissodesmus* and *Tasmanodesmus* parapatry, since the five species concerned are known to flourish in a wide variety of forest and scrub habitats across their respective ranges. It seems more likely that the parapatric species pairs compete in some way, and exclude each other from areas where either could exist in the absence of a competitor. Explanations of this kind have been advanced for parapatry in freshwater crayfish (Flynn and Hobbs, 1984) and frogs (Odendaal and Bull, 1982). A postglacial origin for parapatry by secondary contact between subspecies has been suggested for the grasshopper *Chorthippus parallelus* in the Pyrenees (Cooper and Hewitt, 1993). Parapatry between less closely related millipedes in the Weavers Creek area may have arisen in the Holocene in a similar way, since the area experienced periglacial conditions in the late Pleistocene and probably lacked tree cover. On the other hand, geological evidence (see above) indicates that the general form of the landscape in the Weavers Creek area has changed little over

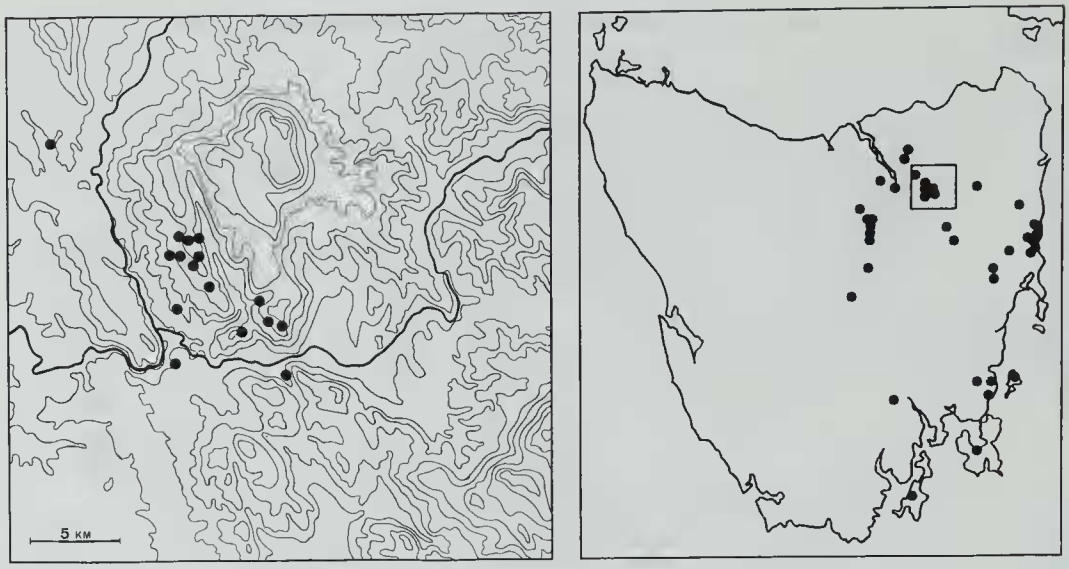

Figure 12. As Fig. 7, for paradoxosomatid n. gen., n. sp.

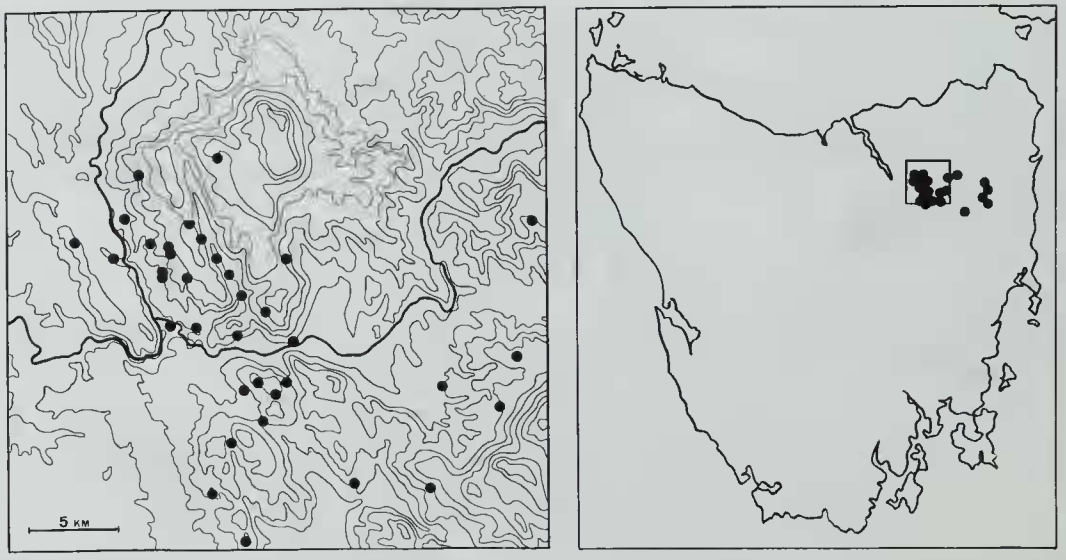

Figure 13. As Fig. 7, for dalodesmid n. gen. 2, n. sp. 2.

millions of years. Millipedes in the area may therefore have been parapatric well before the ice ages, and their parapatry may have been interrupted and re-established during glacial and interglacial times, respectively. This notion is in accord with the hypothesis that *Lissodesmus* n. sp. NE3 is a stabilised hybrid derived from a previous *alisonae*/E1 contact period, and now persisting as a relict at two disjunct locations in north-east Tasmania. Molecular phylogenetic studies of Tasmanian dalodesmids will shed light on these historical-biogeographical questions. Questions concerning the location of the Weavers Creek overlap zone — whether and in which direction it may be moving, and where it was in the Tertiary and Pleistocene interglacials — are unanswerable.

Conservation

The Weavers Creek section of the East Tamar Break is a remarkable biogeographical feature, but there is little else to recommend it as an area worthy of conservation. It is not known to

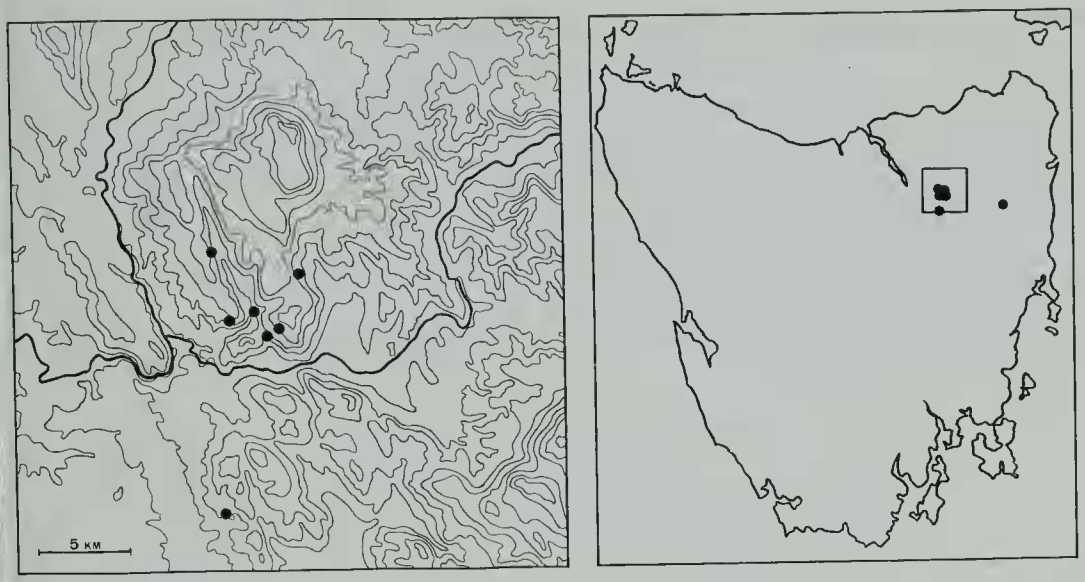

Figure 14. As Fig. 7, for *Lissodesmus* n. sp. NE3.

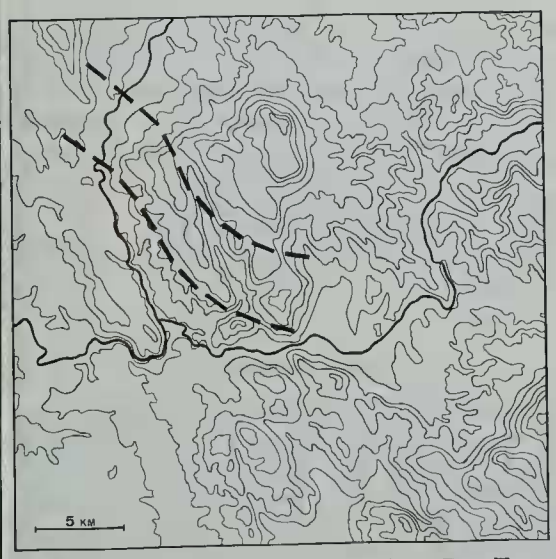

Figure 15. Approximate location of the East Tamar Break in the Weavers Creek area, as defined by millipede range boundaries

harbour a concentration of rare and unusual terrestrial invertebrates, the only rare species collected there to date being the millipede *Lissodesmus* n. sp. NE3. North-east of the area is the c. 2000 km^2 'centre of endemism' known as Plomleys Island (Mesibov, 1994a), but the Weavers Creek overlap zone lies on its margin and at least one Plomleys Island endemic, the millipede *Gasterogramma* n. sp. 5, has not yet been found in the Weavers Creek catchment. Forest vegetation in the zone is typical for the area. A 779 ha block of State forest at the southern end of Weavers Ridge is a proposed Forest Reserve (B. Farmer, Forestry Tasmania, pers. comm.), but the block was first selected as a Recommended Area for Protection because it is a regionally representative area of dry eucalypt forest (Brown and Hickey, 1990).

There is also little evidence that millipedes in the zone require special protection. It is no harder to find litter invertebrates, generally, in recently logged areas on Weavers Ridge than in adjoining unlogged forest An intense wildfire in December, 1994 burned through most of the proposed Forest Reserve on Weavers Ridge, but the dry forest vegetation is recovering well and millipedes can still be found in the burned area. The 'robustness' of litter fauna on Weavers Ridge is almost certainly due to the extensive cover of dolerite debris; litter can accumulate in spaces between and below the rocks, and litter invertebrates can shelter there from fire and logging disturbance. In contrast, on the nearby Tressick Hills millipedes are more or less restricted to patches of rock-mantled ground, while sparsely grassed intervening areas are heavily disturbed by sheep. The rock cover on Weavers Ridge also provides insurance against clearance for agriculture and forest plantations.

It is nevertheless possible that non-litter species occur in tight parapatry on Weavers Ridge, and for this reason alone there is a case to

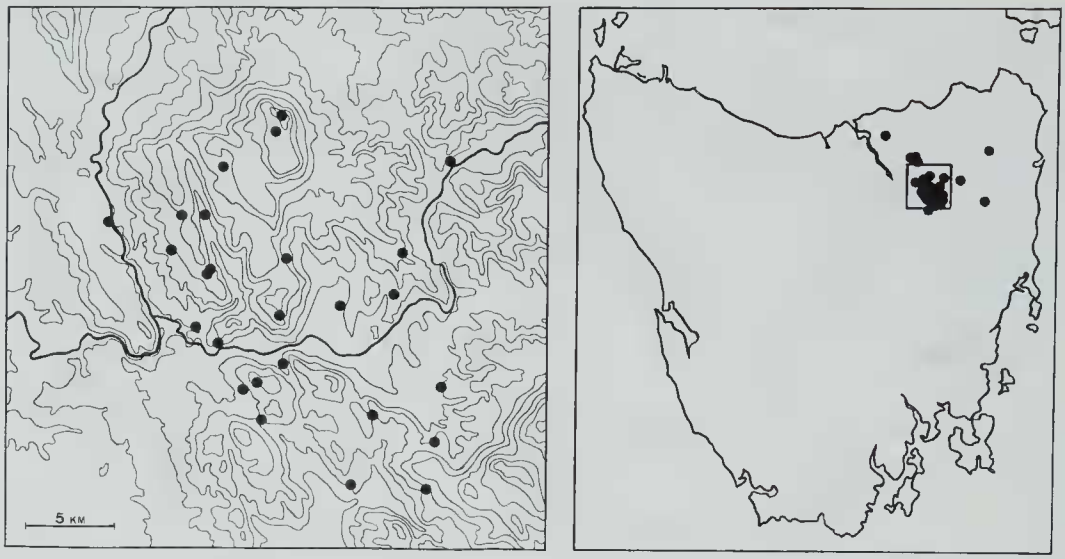

Figure 16. As Fig. 7, for *Tasmanophilus* n. sp.

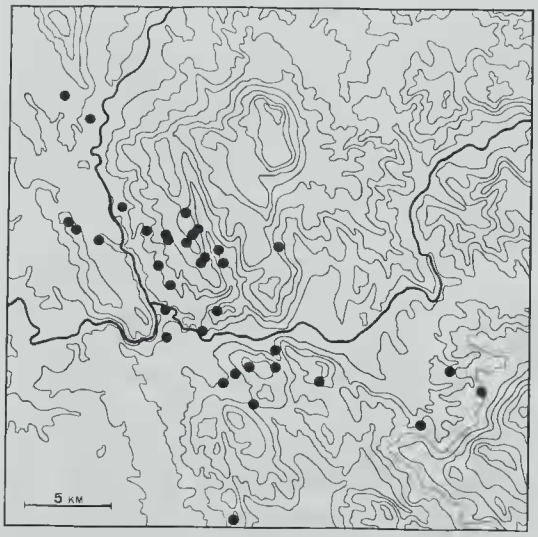

Figure 17. Distribution of *Tasmanophilus 'opinatus'* group (see text) in the study area.

be made for special recognition and gentle handling of the Weavers Creek area. Bull (1991) has suggested that parapatry may have been a more common phenomenon before natural habitats were fragmented by clearance. In Tasmania, the Weavers Creek parapatric zone is the narrowest so far discovered, and its location in lightly disturbed forest increases its value for field studies of the mechanisms by which parapatric boundaries are maintained. The tenure of the area concerned is almost entirely State forest. Local Forestry Tasmania staff have been briefed on sampling results and are prepared to consider special management of a zoogeography study area at Weavers Creek (B. Farmer, pers. comm.). To upgrade the conservation status of the area, sampling and field research results for invertebrate groups other than millipedes and centipedes are needed.

Acknowledgements

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